Human Motion Perception and Smooth Eye Movements Show Similar Directional Biases for Elongated Apertures

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Although numerous studies have examined the relationship between smooth-pursuit eye movements and motion perception, it remains unresolved whether a common motion-processing system subserves both perception and pursuit. To address this question, we simultaneously recorded perceptual direction judgments and the concomitant smooth eye-movement response to a plaid stimulus that we have previously shown generates systematic perceptual errors. We measured the perceptual direction biases psychophysically and the smooth eye-movement direction biases using two methods (standard averaging and oculometric analysis). We found that the perceptual and oculomotor biases were nearly identical, suggesting that pursuit and perception share a critical motion processing stage, perhaps in area MT or MST of extrastriate visual cortex. Published by Elsevier Science Ltd.

Pursuit   Area MT   Barberpole illusion   Models   Direction perception

INTRODUCTION

Humans are reliably able both to discriminate the perceived direction of moving patterns (for a review, see Thompson, 1993) and to track the motion with smooth-pursuit eye movements (for reviews, see Lisberger, Morris & Tychsen, 1987; Heinen & Keller, 1991). How are these abilities related? Clearly, both begin with the same visual input, the dynamic intensity variations of the image on the retina. Both abilities require processing of this input signal to extract a motion signal which is then used to generate either a psychophysical decision or an eye movement. The question we address here is whether the brain performs these tasks using separate pathways or are they both performed using a common motion-processing stage.

Both possibilities exist in primates, as there are at least two anatomically distinct pathways that carry visual-motion information and that generate smooth eye movements: one cortical and one subcortical. The phylogenetically older subcortical pathway, the accessory optic system (AOS), begins with directionally selective ganglion cells which project directly to a number of brainstem nuclei which, in turn, project to ocular motoneurons via brainstem premotor nuclei. This subcortical pathway is clearly involved in the OptoKinetic Reflex (OKR) in

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lower mammals (for a review, see Simpson, 1984) as well as in humans and other primates (Cooper & Magnin, 1986; Fredericks, Giolli, Blanks & Sadun, 1988; Fuchs & Mustari, 1993).

The more evolutionarily recent cortical pathway has become prominent in primates with a stream of visual areas starting in primary visual cortex (V1) and proceeding through the middle temporal (MT) and medial superior temporal (MST) areas, and also projecting to the frontal eye fields (FEF) (van Essen, Maunsell & Bixby, 1981; Maunsell & van Essen, 1983; Ungerleider, Desimone, Galkin & Mishkin, 1984; Ungerleider & Desimone, 1986; Boussaoud, Ungerleider & Desimone, 1990; for a review, see Maunsell & Newsome, 1987). The cortical pathway accesses brainstem oculomotor structures via the pons and the cerebellum (Glickstein, Cohen, Dixon, Gibson, Hollins, Labossiere, *et al.*, 1980; Glickstein, May & Mercier, 1985; Glickstein, Gerrits, Kralj-Hans, Mercier, Stein & Voogd, 1994; Maunsell & van Essen, 1983; Ungerleider *et al.*, 1984; Langer, Fuchs, Chubb, Scudder & Lisberger, 1985a; Langer, Fuchs, Scudder & Chubb, 1985b; Yamada & Noda, 1987; Tusa & Ungerleider, 1988; Leichnetz, 1990; Boussaoud, Ungerleider & Desimone, 1992; Thielert & Thier, 1993). The cortical inputs to this pathway have been shown to play a critical role in pursuit. There is a well documented correlation between the neuronal responses and smooth eye movements (Sakata, Shibutani & Kawano, 1983; Kawano, Sasaki & Yamashita, 1984; Komatsu & Wurtz, 1988; Newsome, Wurtz & Komatsu,

1988; Erickson & Dow, 1989; MacAvoy, Gottlieb & Bruce, 1991). Electrical stimulation produces smooth eye movements (Komatsu & Wurtz, 1989; Gottlieb, Mac-Avoy & Bruce, 1994). Lesions cause deficits in smooth eye movements (Newsome, Wurtz, Dürsteler & Mikami, 1985; Dürsteler, Wurtz & Newsome, 1987; Dürsteler & Wurtz, 1988; Lynch, 1988; Keating, 1991). Furthermore, this pathway is probably involved not only in "voluntary" pursuit but also in "reflexive" short-latency ocular following (Miles, Kawano & Optican, 1986; Gellman, Carl & Miles, 1990; Kawano, Shidara, Watanabe & Yamane, 1994).

Single-unit recording, electrical stimulation, and lesion studies also demonstrate that MT and MST are specifically involved in motion perception (Newsome & Pare, 1988; Salzman, Britten & Newsome, 1990; Salzman, Murasagi, Britten & Newsome, 1992; Britten, Shadlen, Newsome & Movshon, 1992; Murasugi, Salzman & Newsome, 1993; Celebrini & Newsome, 1994, 1995; Pasternak & Merigan, 1994). Thus, while many studies have shown that MT and MST are involved in pursuit and others have shown that they also are involved in perception, because none of the studies assessed their contributions to perception and pursuit simultaneously, it remains unclear if and how these two functions are related. Furthermore, no information is available on the role, if any, the AOS plays in perception and little is known of its role in pursuit. Finally, the breakdown of the simple dichotomies of cortical–subcortical, voluntary–reflexive, conscious–unconscious in primates makes it even harder to resolve the link between motion perception and smooth eye movements. Multiple parallel mechanisms for the processing of visual motion, some controlling pursuit and others determining perception remain a possibility (see Goodale & Milner, 1992).

The human psychophysical literature is divided on this issue. While some have argued that the visual motion input for pursuit is shared with that for perception (Yasui & Young, 1975; Steinbach, 1976; Wyatt & Pola, 1979; Kowler & McKee, 1987; Pola & Wyatt, 1989; Ringach, Hawken & Shapley, 1996; Stone, Beutter & Lorenceau, 1996a), others have argued that the visual input for pursuit is retinal slip independent of perceived motion (Mack, Fendrich & Pleune, 1979; Mack, Fendrich & Wong, 1982; Zivotofsky, Averbuch-heller, Thomas, Das, Discenna & Leigh, 1995). We address this question by examining the quantitative relationship between the perceived direction of a moving stimulus and the direction of the smooth eye movement it produces, using stimuli for which aperture shape has previously been shown to produce systematic errors (biases) in the perceived direction of motion (Beutter, Mulligan & Stone, 1996b). If eye movements and perceptual judgments share a common cortical motion-processing stage, then, whenever one is biased, one would expect the other to be biased in a quantitatively similar manner. To investigate this possibility, we simultaneously measured the perceived direction of motion and the direction of the

smooth eye-movement response to a moving plaid viewed through an elongated aperture. We then compared the observed biases in the perceptual and oculomotor responses.

METHODS

Observers

Three observers participated in this experiment, the two authors and one non-naïve observer. All observers had experience making directional judgments and each had normal or corrected to normal vision. Before data collection began, the observers practiced making the psychophysical judgments and tracking the stimulus in preliminary runs.

Task

We simultaneously measured observers' eye-movement and psychophysical responses to plaids drifting in either elongated or circularly symmetric windows. Observers were instructed to track the plaid stimulus and to determine whether the plaid appeared to be moving rightward or leftward of straight down. On each trial, the eye movements were recorded and observers pressed a button indicating their right/left decision.

Stimuli

We used "Type I", symmetric, orthogonal, equal spatial and temporal frequency plaids, because they cohere well (Adelson & Movshon, 1982). Specifically, the stimulus, $I(\vec{x}, t)$, was a drifting plaid windowed by a spatial gaussian:

$$I(\vec{x}, t) = I_0[1 + cP(\vec{x}, t)W(\vec{x})] \qquad (1)$$

where

$$P(\vec{x}, t) = \sin[2\pi(\vec{f}_s \cdot \vec{x} + f_t t)] + \sin\left[2\pi(\vec{f}_s^{\perp} \cdot \vec{x} + f_t t)\right] \qquad (2)$$

and

$$W(\vec{x}) = \exp\left(-\frac{(\vec{x} \cdot \vec{e})^2}{2\sigma_H^2} - \frac{(\vec{x} \cdot \vec{e}^{\perp})^2}{2\sigma_W^2}\right). \qquad (3)$$

The plaid was the sum of two orthogonal ($\vec{f}_s \cdot \vec{f}_s^{\perp} = 0$)sine-wave "component" gratings moving with equal speeds. Both gratings had equal spatial ($|\vec{f}_s| = |\vec{f}_s^{\perp}| = 0.6$ c/d) and temporal ($f_t = 4$ Hz) frequencies, and equal peak contrast ($c = 0.25$). The mean luminance (I_0) was fixed at 42 cd/m². The gaussian spatial window had standard deviations, σ_H (height) and σ_W (width), in the two principal directions, $\vec{e}$ and $\vec{e}^{\perp}$, respectively. For the elongated windows, the standard deviations were unequal and the orientation of the window was defined as the direction of the long axis, $\vec{e}$, relative to the plaid direction of motion. We defined the orientation of the circularly symmetric window to be 0 deg. The stimulus was turned on and off abruptly and its duration was 600 msec.

We used three types of spatial gaussian windows:

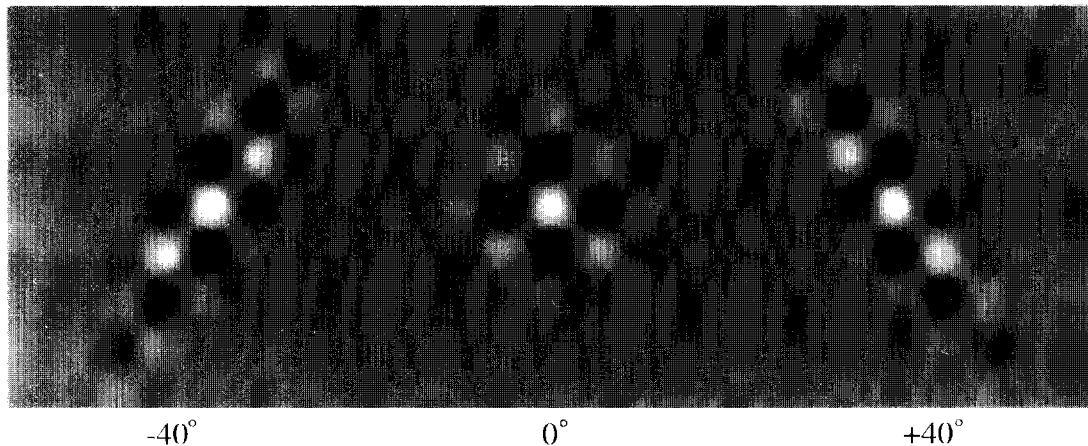-40°   0°   +40°

FIGURE 1. Static examples of the three window conditions. In each, the plaid orientation is 0 deg.

elongated and tilted with either a +40 deg or a -40 deg orientation, and circularly symmetric. For the elongated windows, σ_{ll} was 2.5 deg and σ_W was 0.625 deg, which corresponds to an aspect ratio (σ_{ll}/σ_W) of 4. For the circularly symmetric window, we set both σ_{ll} and σ_W to 1.25 deg, so that the total window area was approximately the same for all three window types. Static illustrations of the stimulus conditions are shown in Fig. 1. For each window type, the 0 deg plaid direction was defined as straight downward. The other motion directions were produced by rotating the entire stimulus (both plaid and window). While this method results in the stimulus containing static orientation cues to the direction of motion, it is unlikely that this affected our results because: (1) observers were instructed to judge the perceived direction of motion; (2) the orientation cues were identical for the +40 deg and -40 deg windows, so cannot underlie the observed differences in biases produced by the window tilt; and finally (3) the use of these cues would tend to reduce rather than cause a direction bias. In our previous study (Beutter et al., 1996b), we also performed a control experiment in which the orientation remained fixed and only the temporal frequencies of the plaid components were changed to effect the change in the plaid direction of motion. This eliminated the static orientation cues (although it produces a different set of caveats), yet resulted in similar perceptual biases.

The stimuli were displayed on a 19″ Barco[R] color monitor (model CDCT 6351B) using the AT Vista[R] video display system hosted by an IBM[R] 486. The monitor was run in the interlaced 60-Hz refresh-rate mode. To minimize interlace artifacts, alternate horizontal lines were set equal to one another by computing a 320 × 243 pixel image and zooming it by a factor of two in both the horizontal and vertical directions so that it filled the 640 × 486 display region. The display pixel sizes were 0.47 mm horizontally and 0.54 mm vertically. At the 57-cm viewing distance, the full display subtended

30 deg × 26 deg. The luminance output of the monitor was calibrated to correct for its gamma nonlinearity using a look-up table. The plaid motion was produced using a dithering animation method which is described in detail elsewhere (Mulligan & Stone, 1989).

Experimental procedures

Trials began with the presentation of a 1 deg by 1 deg fixation cross at the center of the screen for 500 msec. The fixation cross was then extinguished and the stimulus was presented. For each window angle (-40, 0 and +40 deg), we presented five different plaid directions of motion using the method of constant stimuli. Our previous work (Beutter et al., 1996b) showed that the elongated windows bias the perceived direction of motion toward the long axis of the window by ~10–15 deg. Therefore, to ensure that we obtained full psychometric functions, for each window angle we adjusted the range of plaid directions so that they were approximately centered on perceived straight down. For the 0 deg window, we used plaid directions of -10, -5, 0, 5 and 10 deg. For the -40 deg window, we used plaid directions of 0, 5, 10, 15, and 20 deg. For the +40 deg window, we used plaid directions of -20, -15, -10, -5, and 0 deg. Each run consisted of 120 counterbalanced trials (eight trials for each of the 15 conditions produced by the three window angles and five plaid directions). Each observer ran a minimum of three runs.

Psychophysical data

We analyzed the psychophysical data for each window angle by fitting a cumulative gaussian to the proportion of the trials judged to move rightward as a function of the plaid direction of motion. The proportion rightward for each window angle and plaid angle was computed after combining the data across runs for each observer. We weighted each point by its expected uncertainty (assuming a binomial response distribution) and computed the minimum chi-squared fits to the data. A positive bias (to
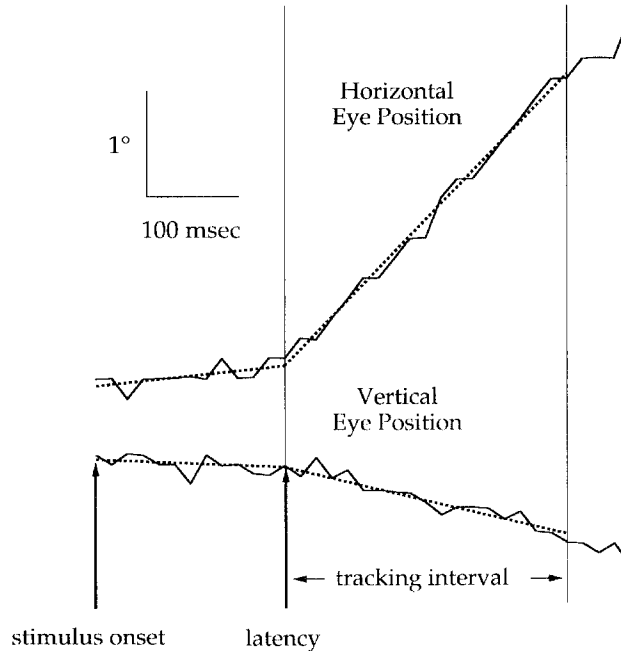
FIGURE 2. Sample eye-movement data from a single trial. The horizontal and vertical calibrated eye-position traces are shown as solid lines. The fits are shown as dotted lines. Each trace was fit with two line segments which were constrained to have the same value at the eye-movement onset. For this trial, the eye-movement latency is 200 msec and the direction is −13 deg.

the right) in the perceived plaid direction means that the plaid is perceived as moving more rightward than it actually is. However, the resulting increase in the proportion of rightward responses produces a leftward shift of the psychometric functions. Thus, we defined the psychophysical bias to be the negative of the offset of the best-fitting cumulative gaussian, and defined the threshold to be its standard deviation. The bias is therefore the negative of the plaid direction that produces 50% rightward judgments, and the threshold is the difference in direction between the stimuli corresponding to 50% and 84% rightward judgments.

Oculomotor data

Eye tracking. We measured observers' eye movements with an infrared (IR) video-based eye tracker (ISCAN RK-426) running at 60 Hz, synchronized with our display monitor. Head movements were minimized by using a bite bar. Observers viewed the stimulus monocularly using their left eye with a patch covering their right eye. The experiments were run in a dimly lit room, and the observer viewed the stimulus through a mirror which transmitted visible light but reflected IR. An IR light source illuminated the observer's left eye. For each frame, the eye tracker computes the x and y positions of the pupil in uncalibrated eye-tracker coordinates.

Calibration. Prior to every run, we performed a calibration by having observers fixate a series of nine crosses arranged in a 2 deg × 2 deg grid. The crosses

were presented in a fixed pseudorandom order and each was shown twice. The crosses were each presented for 1.5 sec, and the eye-movement recording began after 0.5 sec and lasted 1.0 sec. For each fixation, the mean eye position and its standard deviation were calculated. To ensure the fixations were not contaminated by blinks, eye positions more than 5 standard deviations away from the mean were eliminated and the means and standard deviations were recomputed iteratively. The standard deviations provide an estimate of the eye-tracker noise which averaged 0.13 deg and 0.15 deg in the horizontal and vertical directions, respectively. To convert the raw eye-tracker output (T_x, T_y) to the actual eye position (E_x, E_y), the calibration data for all of the fixations were fit to the model:

$$E_x = G_{xx} \cdot T_x + G_{xy} \cdot T_y + X_0 \qquad (4)$$

$$E_y = G_{yx} \cdot T_x + G_{yy} \cdot T_y + Y_0 \qquad (5)$$

where the fit parameters are G_{xx} (horizontal gain), G_{xy} (V-to-H cross term), X_0 (horizontal offset), and G_{yx} (H-to-V cross term), G_{yy} (vertical gain), Y_0 (vertical offset). Within the narrow range of eye movements examined (±2 deg), the calibration data were fit well by this linear six-parameter model.

Saccade detection. For each trial, we recorded the observer's eye movements and converted the raw x and y tracker outputs to the calibrated horizontal and vertical eye positions using the above equations. We checked

each trial for the presence of saccades and discarded trials in which a saccade was initiated within the first 400 msec. Because the stimulus was a moving pattern and not a small spot, most trials were saccade free (98%, 92%, and 68% for observers PV, BB, and LS, respectively). To detect saccades, estimates of the horizontal and vertical accelerations were first calculated using a digital filter (1, 1, 1, 1), a low-pass filtered double-differentiator (3 dB cut-off at 26 Hz). The accelerations were then weighted by estimates of their respective noises (obtained from the calibration data) and finally the sum of their squares was compared with a threshold. We determined the threshold by examining a large number of trials and comparing our subjective judgments of saccade occurrences with those detected by our objective procedure. This method detected every saccade that we did subjectively, but occasionally indicated additional saccades. This procedure detected saccades of 0.75 deg or greater, but may have missed smaller saccades.

Computation of smooth eye-movement direction. A typical pair of saccade-free horizontal and vertical traces, along with their fits is shown in Fig. 2. To estimate the smooth eye-movement direction, we used the slopes of the x and y responses. To determine the slopes, we defined two intervals for each trial, an initial interval of variable length before the eye movement began and a tracking interval. The tracking interval was 300 msec, unless the first saccade occurred between 400 and 600 msec. For these few trials, the tracking interval ended at the start of the saccade and therefore could be less than 300 msec, but the trial was discarded if the tracking interval was less than 200 msec. For both traces and intervals, the best-fitting lines and their associated χ^2's were computed. A total χ^2 for each putative latency (the length of the first interval) was computed as the sum of the χ^2's of all four fits. Initially, we chose the fit producing the lowest total χ^2, but further examination showed that for a few trials, the tracker noise caused the total χ^2 to be very similar for a range of latencies. To reduce the effects of this noise, we computed the median latency (183 msec), and added a small term penalizing shorter and longer latencies. The penalty was proportional to the square of the difference in latency from the median with the constant of proportionality (0.27) chosen, such that the penalty term was small relative to the expected variation in the total χ^2. The best fits were then determined by minimizing the sum of the total χ^2 and the penalty term. The direction of the smooth eye-movement response for each trial was then computed as the arctangent of the ratio of the slopes of the best-fitting lines to the horizontal and the vertical traces in the tracking interval. The direction uncertainty was computed from the uncertainties in these slopes. Before combining the smooth eye-movement data across runs, it was necessary to eliminate small overall rotations (approximately ⊥3 deg) introduced by variations in the calibrations across runs. To do this, for each run, we subtracted the mean smooth eye-movement direction for that run from the direction for each trial. The mean

smooth eye-movement direction for each run was calculated by first computing, for each condition, the average direction across trials (weighted by each trial's uncertainty) and then calculating the unweighted average across conditions. We then analyzed these directions further using the two techniques described below.

Average eye-movement analysis. For each condition, we computed the average smooth eye-movement direction and its standard deviation across runs. For each window angle, a line was then fit to these data by weighting each point by its uncertainty (computed from its standard deviation) and minimizing χ^2. We defined the smooth eye-movement bias to be the negative of the plaid direction that corresponded to a straight-down eye-movement (0 deg). A positive bias (to the right) results in a more rightward smooth eye movement and therefore causes the plaid direction corresponding to a straight-down eye movement to shift to the left.

Oculometric analysis. We also analyzed the eye-movement direction data using an oculometric decision model similar to that used by Kowler and McKee (1987) to examine pursuit speed. Our oculometric decision model makes a rightward/leftward decision on each trial by examining only the smooth eye-movement record, without knowledge of the stimulus or the perceptual decision. It is based on signal-detection theory and parallels the psychophysical decision process. In signal-detection theory, the psychophysical data are modeled as resulting from a decision based on noisy signals. In a simple version, each stimulus undergoes noisy processing, which results in a single number that depends on the stimulus direction of motion, but is contaminated by additive gaussian noise. The rightward/leftward perceptual response is determined by a decision stage that compares this number to a decision threshold. Our oculometric decision model is identical to this, except that it acts on the smooth eye-movement direction. It produces an oculometric function similar to the standard psychometric function. For each trial, the oculometric decision model ascertains whether the smooth eye movement for each trial was rightward or leftward of straight down (this corresponds to setting the decision threshold to 0 deg). If the direction is to the right of straight down, a rightward decision is made for that trial, and correspondingly if the direction is to the left of straight down, a leftward decision is made. Then, for each condition, the proportion of rightward decisions is calculated to compute the value of the oculometric function. The average oculometric data were computed by combining the data for each observer across runs. Because the oculometric functions were similar to the psychometric functions, we also fit them with cumulative gaussians. We weighted each point by its expected uncertainty (assuming a binomial distribution) and computed the minimum χ^2 fits to the data. As with the psychophysical data, the oculometric bias was defined to be the negative of the offset of the best-fitting cumulative gaussian and the threshold was defined to be its standard deviation.
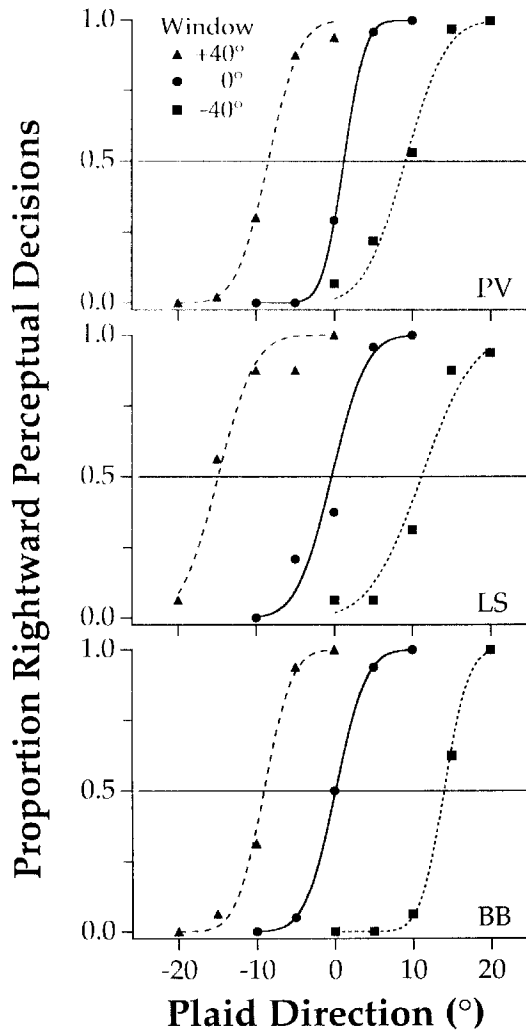
FIGURE 3. The psychophysical data for the three observers. The average proportion judged rightward for each of the three window angles (+40 deg, triangles; 0 deg, circles; -40 deg, squares) is plotted as a function of the plaid direction of motion. The lines through the data are the best-fitting cumulative gaussians.
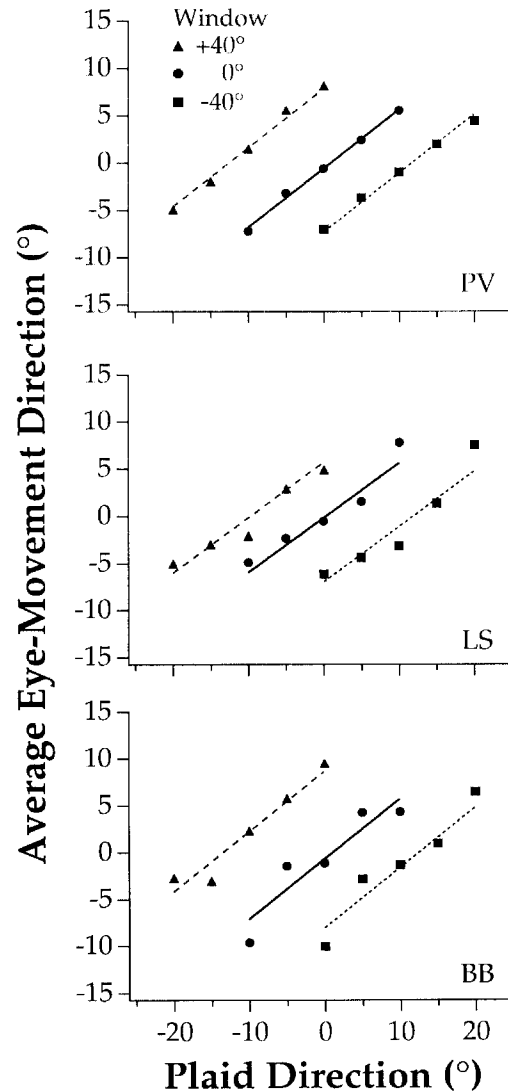

FIGURE 4. The average eye-movement data for the three observers. The average eye-movement direction for each of the three window angles (+40 deg, triangles; 0 deg, circles; -40 deg, squares) is plotted as a function of the plaid direction of motion. The lines through the data are the best linear fits.

RESULTS

Psychometric results

The psychophysical data for the three observers are shown in Fig. 3, in which the proportion judged rightward is plotted as a function of the plaid direction for the three window angles. The results for the three observers are similar. The psychometric function for the +40 deg window is shifted to the left, while that for the -40 deg window is shifted to the right by an approximately equal amount relative to the 0 deg window data. Thus, the elongated windows bias the perceived direction of plaid motion toward the long axis of the window. To quantify the bias and uncertainty, we fit the psychophysical data for each window angle to a cumulative gaussian.

The psychophysical direction biases for all three observers are shown in Fig. 7 (top panel) and averaged -11.4 ± 2.8 deg for the -40 deg window, -0.3 ± 0.4 deg for the 0 deg window, and 10.7 ± 3.0 deg for the $+40$ deg window ($\pm$SD across observers). The thresholds (a measure of perceptual uncertainty) for the three window types were similar. The thresholds averaged over observers for the -40, 0, and $+40$ deg window angles were 3.3 ± 0.3 deg, 2.9 ± 0.5 deg, and 4.0 ± 1.0 deg, respectively. These data show that the elongated windows produce systematic biases in the perceived direction without a change in the perceptual uncertainty.
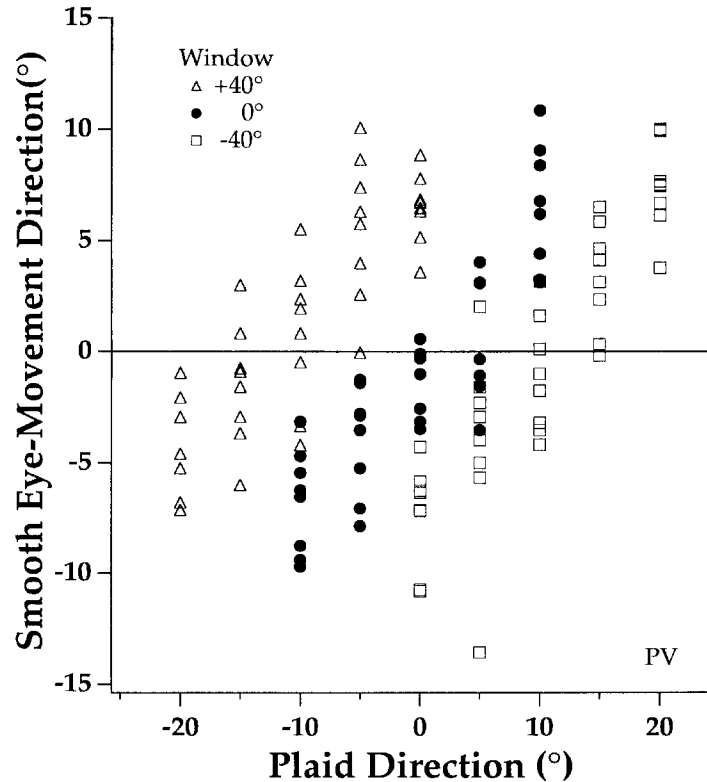
FIGURE 5. The raw eye-movement direction data for observer PV for a single run. The eye-movement direction on each trial is plotted as a function of the plaid direction of motion. The data for the +40, 0, and −40 deg window angle are shown as the open triangles, filled circles, and open squares, respectively. The horizontal line corresponding to an eye-movement direction of zero represents the oculomotor decision threshold.

Average eye-movement direction results

The smooth eye-movement data for the three observers are shown in Fig. 4, in which the average smooth eye-movement direction is plotted as a function of the plaid direction for the three window angles. Similar to the psychophysical results, the eye-movement data for the +40 deg window are shifted to the left, while those for the −40 deg window are shifted to the right by an approximately equal amount relative to the 0 deg window data. To quantify these oculomotor biases, we fit the average data for each window angle to a straight line and defined the direction bias as the negative of direction producing a straight downward eye movement. The slopes of the best-fitting lines were similar across observers and conditions (the mean ± SD was 0.63 ± 0.04). The biases, shown in Fig. 7 (middle panel), were similar for the three observers and averaged −12.0 ± 2.4 deg for the −40 deg window, −0.7 ± 0.9 deg for the 0 deg window, and 11.9 ± 1.3 deg for the +40 deg window.

Oculometric results

The smooth eye-movement direction data from each

trial of a single run for observer PV are shown in Fig. 5. Examining the +40 deg data, one can see that for a plaid direction of −20 deg, this observer always produced smooth eye movements that were leftward of straight downward (the eye-movement directions were < 0 deg). Thus, these data correspond to an oculometric proportion rightward of 0%. Similarly, for the +40 deg window and 0 deg plaid direction (straight down), this observer always produced smooth eye movements that were rightward of straight down (the eye-movement directions were >0 deg), and thus these data correspond to an oculometric proportion rightward of 100%. For intermediate values of plaid direction, an intermediate percentage of the smooth eye-movement directions was rightward. From these raw data, it is clear that the +40 deg window produced a rightward bias in the smooth eye movements (the eye movement is more rightward than the stimulus) and similarly that the −40 deg window produced a leftward bias (the eye movement is more leftward than the stimulus). A similar analysis was performed for all conditions and observers, and the oculometric functions were fit with cumulative gaussians to provide quantitative measures of the bias and uncertainty.
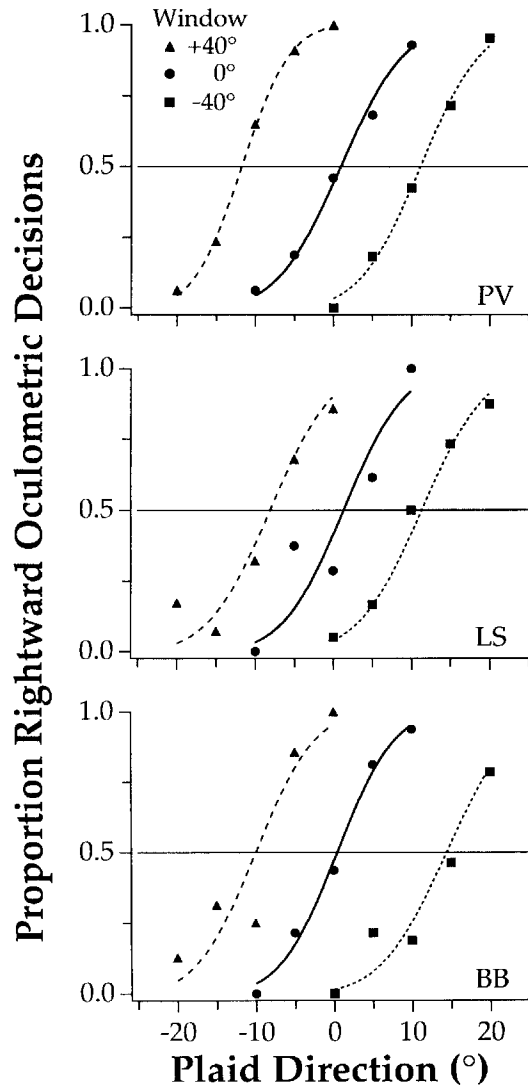
FIGURE 6. The oculometric data for the three observers. The oculometric proportion rightward for each of the three window angles (+40 deg, triangles; 0 deg, circles; −40 deg, squares) is plotted as a function of the plaid direction of motion. As for the psychophysical data, the lines through the data are the best-fitting cumulative gaussians.
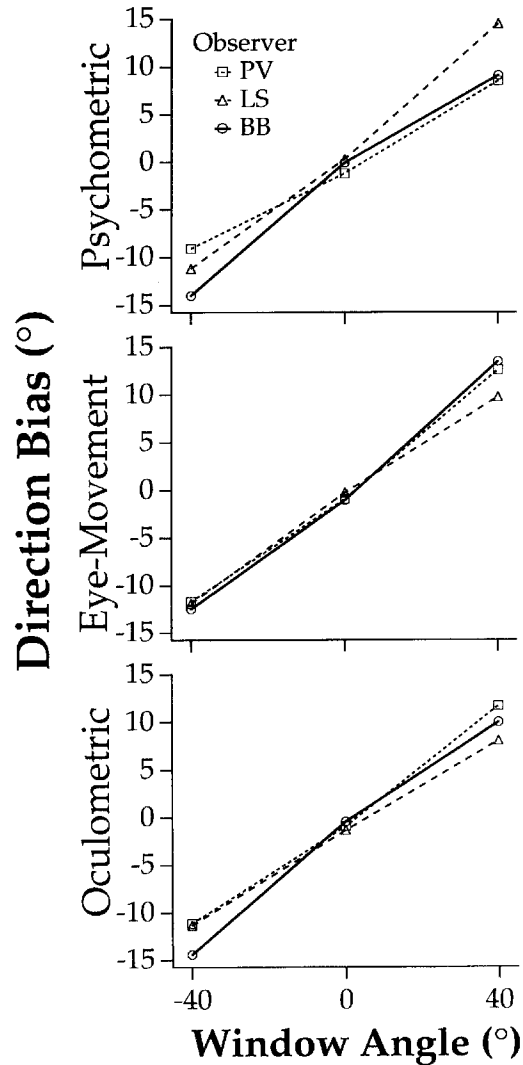

FIGURE 7. The direction biases as a function of the window angle for the three observers. The top panel shows the direction biases computed from the psychophysical data, the middle panel shows the direction biases computed from the average eye-movement data, and the bottom panel shows the direction biases computed from the oculometric data.

The oculometric data for the three observers are shown in Fig. 6, in which the proportion judged rightward is plotted as a function of the plaid direction for the three window types. The data from all observers were similar. The oculometric function for the +40 deg window is shifted to the left, while that for the −40 deg window is shifted to the right by an approximately equal amount with respect to that for the circularly symmetric window. The oculometric biases for all three observers are shown in Fig. 7 (bottom panel) and averaged −12.3 ± 1.7 deg for the 40 deg window, −0.9 ± 0.3 deg for the 0 deg

window, and 9.9 ± 2.2 deg for the +40 deg window. The thresholds for the three window angles were similar: 6.4 ± 0.4 deg, 6.1 ± 0.3 deg, and 5.7 ± 0.5 deg averaged over observers for the −40, 0, and +40 deg window angles, respectively.

Open-loop analysis

We were interested in examining the open-loop pursuit response because this portion of the response reflects the visual processing for pursuit prior to the point where feedback confounds the issue (Lisberger & Westbrook, 1985). However, we were constrained by the limits imposed by both the noise and resolution of the eye
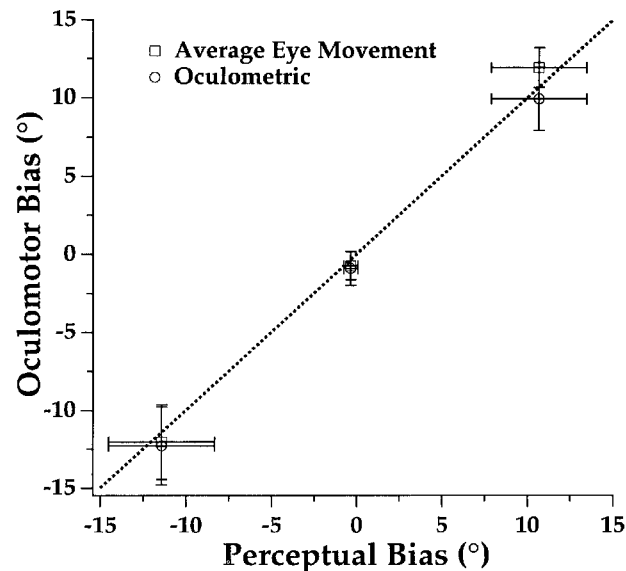
FIGURE 8. Data summary. The average eye-movement biases (squares) and oculometric biases (circles) are compared with the perceptual biases for the three window angles. The data for each method have been averaged over observers. The error bars represent the standard deviation across observers. The dotted line has unity slope and intercept zero and corresponds to equal perceptual and oculomotor biases.

tracker. We chose to fit the eye-movement data over an interval of 300 msec, which is longer than our estimate of the actual open-loop interval from the response latency (183 msec). To ensure that our choice of the near open-loop interval did not significantly contaminate our results, we re-examined the data for one observer, PV, by fitting only the first 183 msec of the pursuit response. We found that, as expected, the noise levels increased significantly (the average estimated uncertainty in direction approximately doubled), but the directions changed by only ~2 deg (average of the unsigned difference over all trials), which is small compared with the observed biases of more than 10 deg. Thus, while fitting over a shorter interval would have made our data much noisier (the uncertainty decreases approximately as the length of the interval to the 3/2 power), it would not have substantially changed our results.

Entire eye-movement analysis

For each trial, we obtain a single psychophysical response, rightward or leftward, while we have 600 msec of eye-movement data. We assumed that the direction of the eye movement was approximately constant over the 300 msec tracking interval and thus fit the data to straight lines, obtaining a single average direction for each trial. The psychophysical response, however, may be based on the entire duration of the stimulus or any part thereof. We verified that the eye-movement direction remained approximately constant by comparing the fits to the initial 300 msec with those of the entire recorded eye movement for one observer, PV. We found that the average over all trials of the unsigned direction difference

was small, ~1 deg. Therefore, comparing the entire eye movement with the percept would have produced similar biases.

Saccadic contamination

Our saccade detection procedure detected saccades of 0.75 deg or greater. Because of eye-tracker noise, decreasing the saccade threshold below this value would cause false saccades to be detected. Nonetheless, to determine if the saccade threshold affected the eye-movement biases, we reanalyzed one run of observer PV and discarded all trials in which a horizontal saccade of 0.2 deg or greater was indicated. This reduced the number of usable trials by 66%, yet the changes in the average eye-movement biases were small (range: −3 to +14%). Under the worst-case scenario, in which we assume the elongated windows produce undetected 0.2 deg saccades that, instead of being in the direction of the percept or the stimulus, are purely horizontal, the maximum bias that could result is less than half that observed. Therefore, the smooth component of the eye-movement response was clearly biased, although it is possible that the saccades were also biased.

Summary

We have simultaneously measured oculomotor and perceptual direction biases for plaid stimuli drifting in elongated spatial windows. The perceptual and eye-movement biases are compared in Fig. 8, which plots the oculomotor biases (both methods) as a function of the perceptual bias for the same window type. The dashed line has unity slope and zero intercept. The fact that all

the points are close to this line indicates that the perceptual and oculomotor biases are nearly identical.

DISCUSSION

We have shown that windowing plaids by elongated spatial gaussians produces quantitatively similar directional biases in both the perceptual decisions and the concomitant oculomotor responses. We simultaneously measured the perceptual biases psychophysically and the pursuit biases using two methods (average eye movement direction and oculometric analysis). The oculometric analysis converted the raw eye-movement response for each trial to a simple rightward/leftward decision, and generated an oculometric function similar to the psychometric function. This allowed us to make a simple direct comparison between oculomotor responses and perceptual decisions. While the three methods used to measure the directional biases produced remarkably similar results, there are two caveats that must be addressed.

Caveats

Overall vertical eye-movement bias. In fitting the average eye-movement data as a function of the plaid direction, we found that the best-fitting lines always had slopes less than 1 and, in fact, averaged 0.63 (Fig. 4). This was surprising because it might be expected that a given change in plaid direction should produce an equivalent change in eye-movement direction, while we found that the average change in eye-movement direction was only about two-thirds of the change in plaid direction. It is possible that the eye-movement directions were affected by the stimulus direction of motion in previous trials. Kowler and colleagues (Kowler & Steinman, 1979; Kowler, 1989, 1990) have shown that pursuit eye movements can be influenced both by the observer's expectations and by the stimulus motion on previous trials. Because our stimuli moved largely straight down with small leftward or rightward components added on some trials, it is possible that the stimulus direction of motion on previous trials might cause the eye-movement direction to tend to be more downward. We also cannot rule out the possibility that the perception of motion was actually biased toward the vertical and caused the observed eye-movement bias. Finally, another possible explanation is that pursuit is simply biased toward the cardinal directions (in this case vertical), independent of the percept.

Threshold data. Both the psychophysical thresholds and oculometric thresholds are approximately constant across window angles, but the psychophysical thresholds (mean: 3.4 deg) are clearly lower than the oculometric thresholds (mean: 6.0 deg). This may be, in part, due to the fact that the percept is likely to be based on the observation of the entire stimulus, while we analyzed the eye-movement direction over a much shorter interval. An additional contribution to the higher oculometric thresholds is directional noise introduced by the eye tracker, which we estimate to be approximately 2 deg. Another possible noise source is pre-motor processing.

Perception and smooth eye movements

Traditionally, studies of oculomotor control have focused on mechanistic models in which the motion of the target on the retina (retinal slip) drives smooth eye movements through a negative feedback loop with various forms of internal positive feedback (e.g. Robinson, Gordon & Gordon, 1986; Krauzlis & Lisberger, 1991; Ringach, 1995). Most present models at least implicitly assume that perception is a separate process which plays no direct role in the generation of pursuit, although higher-order phenomena have been shown to have a major influence (Kowler, 1990). Several studies (Mack *et al.*, 1979, 1982; Zivotofsky *et al.*, 1995; Zivotofsky, Krauzlis, Miles & FitzGibbon, 1997) have investigated this issue by examining variations of the Duncker illusion (Duncker, 1929), in which a small target spot is enclosed within a rectangular frame. These studies show that, although a moving frame or background induces a percept of spot motion in the direction opposite to the frame's motion, the eye movements follow the actual motion of the spot, instead of its perceived motion. They argue that raw retinal slip and not perceived motion provides the visual input for pursuit. However, as discussed by Post & Leibowitz (1985), the results are ambiguous because the net smooth eye-movement response may result from a combination of pursuit and OKR. If the OKR response is largely controlled by the motion of the frame, then because the total smooth eye-movement response is measured (pursuit plus OKR), data similar to those found in these experiments would result, even if pursuit was following the percept. In other words, the perceptual judgments and pursuit may be made relative to an OKR stabilized reference system, while the total eye-movement response is measured with respect to an absolute world reference frame.

Yasui and Young (1975) were among the first to suggest that perceived target motion instead of raw retinal slip might be used to drive pursuit. They found that, during vestibular stimulation in the dark, if observers were asked to follow an afterimage, the smooth eye-movement response was increased relative to that with no afterimage. They suggested that because the afterimage is stationary on the retina (no retinal slip), the change in the eye movements must be due to pursuit of the perceived motion of the afterimage. However, as they pointed out, an alternative explanation is simply that the presence of the target caused an attentional increase in VOR gain, and that pursuit and motion perception were not involved. Steinbach (1976) showed that the eye movements produced in response to the horizontal motion of an object viewed through a narrow vertical slit (producing predominately vertical retinal slip) contained horizontal components and were thus qualitatively consistent with the perceived motion. He also showed the motion of a rolling wagon wheel defined only by two spots on the rim, produced qualitatively similar percepts and eye movements. Although these data show that smooth eye movements are not determined merely by retinal slip and appear to be influenced by the percept,

because the perceived motion and the eye movements were not quantitatively compared, the relative contributions of perceived motion and retinal slip remained unclear. Wyatt and Pola (1979) (Pola & Wyatt, 1989) examined pursuit and perception under sustained open-loop conditions, and found that for identical retinal velocities, when perceived target motion increased, so did the eye-movement response. Again, only a qualitative link between perception and pursuit was established. Furthermore, the possibility exists that the sustained open-loop conditions used might have altered normal pursuit strategies. More recently, Ringach et al. (1996) showed that a kinetic depth-effect stimulus (a series of two-dimensional random-dot images without any disparity cues) can generate a smooth vergence response that actually tracks the perceived (illusory) motion-in-depth of the stimulus. Although their study demonstrates a quantitative link between perceived motion and the smooth oculomotor response, it is unclear how the vergence component of the response is related to pursuit and the conjugate component may have simply been driven by raw retinal slip. Finally, using various manipulations of the coherence of moving plaids or lines, a number of recent studies (Dobkins, Stoner & Albright, 1992; Duncan, Stoner & Albright, 1994; Anstis & Ballard, 1995; Beutler, Lorenceau & Stone, 1996a; Stone et al., 1996a; Beutler & Stone, 1997) have provided preliminary evidence that perceptually coherent stimuli produce eye movements in the pattern direction, while perceptually transparent stimuli produce eye movements in the component directions.

Kowler and McKee (1987) took a different approach to the same question. They compared perceptual speed discrimination with the variability in pursuit speed by developing a new approach, "oculometric analysis". Speed discrimination was measured for a small spot using standard psychophysical methods. Using similar but not identical stimuli, they then asked observers to track a spot and recorded their eye movements. Oculometric analysis was used to predict the discriminability of the different stimulus speeds from the distributions of the eye-movement speeds. The lowest oculomotor thresholds (approx. 600–700 msec after the onset of motion) were nearly identical to the psychophysical thresholds. Although perception and pursuit were not measured simultaneously and the duration of the eye-movement stimuli were much longer (1.0–1.8 sec) than the perceptual stimuli (160–240 msec), these results suggest that "perceptual and oculomotor velocity discrimination thresholds may both be influenced by similar representations of the velocity of the target (p. 1012)". Similarly, Watamaniuk and Heinen (1994) have recently found preliminary evidence for a similar link between the precision in perceived direction and the precision of the direction of the smooth eye-movement response to moving random dots. These two studies provide additional evidence that pursuit and perception share a common motion processing stage.

The present results extend the above findings by documenting a quantitative link between perceptual and oculomotor direction errors measured simultaneously. Our analysis showed that, on average, the perceptual and oculometric biases are similar, but did not compare the perceptual judgment on each trial with its associated oculometric prediction. If the perceptual and oculomotor systems share a critical motion processing stage, then the prediction is that, in addition to being equal on average, the oculometric decision and the actual perceptual decision on each individual trial should be correlated. We have preliminary evidence (Beutler & Stone, 1996) that this is indeed so. We showed that for both plaids and random dots moving straight down, left/right judgments and the concomitant (small) leftward/rightward deviations in smooth eye movements are correlated on a trial-by-trial basis. These results (see also Harris, Lewis & Maurer, 1993) provide further evidence that the perceptual and oculomotor motion processing systems share a common neural substrate.

While there are several potential sites for the shared visual-processing area, because determining plaid direction requires integrating motion information (for a review see Beutler et al., 1996b), it probably occurs subsequent to primary visual cortex (V1). Given that a clear causal link has been established between MT/MST and both motion perception and pursuit (Newsome et al., 1985; Newsome & Pare, 1988; Komatsu & Wurtz, 1989; Salzman et al., 1992; Pasternak & Merigan, 1994; Celebrini & Newsome, 1995), it is likely that the output of these areas is shared by both perception and pursuit. However, it is also possible that the observed perceptual and pursuit biases have their origins in V1, although the direct anatomical projections from V1 to brainstem oculomotor centers are sparse (Glickstein et al., 1985).

Different forms of smooth eye movement: pursuit, OKR, and ocular following

As discussed in the Introduction, there are multiple neural pathways by which visual motion can generate smooth oculomotor responses and three identified oculomotor subsystems that do so: OKR, pursuit, and short-latency ocular following. While pursuit is generally thought to be dominated by the cortical visual pathway (Lisberger et al., 1987), OKR is generally believed to be dominated by subcortical visual pathways through the AOS (Fuchs & Mustari, 1993). Because perception and consciousness are generally thought to be cortical phenomena, pursuit is therefore thought to be voluntary and conscious, while OKR is seen as reflexive and unconscious. However, this oversimplified dichotomy is inconsistent with the finding that ocular following, although probably cortically mediated (Kawano et al., 1994), appears reflexive and unconscious. Any segregation of these smooth oculomotor subsystems is further blurred by the fact that, in primates, there are reciprocal connections between extrastriate cortex and the AOS (Maioli, Squatrito & Domeniconi, 1989; Leichnetz, 1990; Boussaoud et al., 1992) which apparently endow primate AOS neurons with the ability to respond to small

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Our windowed plaid stimuli were not designed to distinguish between the various forms of smooth eye movements or to identify the underlying anatomical pathways. Because observers were instructed to track the motion, we postulate that the response was largely pursuit. However, from the present data, we cannot make any firm claims as to whether the responses were pursuit, ocular following, OKR, or combinations thereof. However, in recent studies which used a stimulus that is unlikely to elicit either OKR or ocular following, we still found a correlation between perceived motion and the smooth oculomotor response (Beutter *et al.*, 1996a; Stone *et al.*, 1996a; Beutter & Stone, 1997).

Implications for pursuit models

Most current models of pursuit either implicitly or explicitly use retinal slip and/or its derivatives as the visual input (e.g. Robinson *et al.*, 1986; Krauzlis & Lisberger, 1991; Ringach, 1995). However, our data are inconsistent with the view that retinal slip alone provides the visual-motion signal for pursuit because, for our elongated window stimuli, the tracking of retinal slip would produce little or no bias (see the predictions of the correlation model in Beutter *et al.*, 1996b). Independent evidence for the inadequacy of retinal slip as the visual input for pursuit has also been provided by the fact humans can track occluded objects even when the retinal slip is different from the object motion (Stone *et al.*, 1996a,b, 1997). Furthermore, manipulations of occlusion and contrast can cause parallel changes in perceived motion and the smooth eye-movement response without any change in the image motion (Beutter *et al.*, 1996a; Stone *et al.*, 1996a; Beutter & Stone, 1997). At the very least, pursuit models must be modified to have a more sophisticated front-end which can perform the spatio-temporal integration which is necessary to recover object motion from element motion during occlusion. Finally, the quantitative similarity between the amplitudes of the oculomotor and perceptual biases reported here and the correlation between the perceived and the eye-movement trajectories found in our occlusion studies suggest that the same spatio-temporal integration supports both perception and smooth eye movements. The responses of some MST neurons (Newsome *et al.*, 1988) appear ideally suited to perform this joint task (see, Fig. 3 of Stone *et al.*, 1996a).

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